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Mucilage or slime formation in the cacti

E. GRACE STEWART

(WITH PLATE 8)

The cellular processes involved in the formation of plant slimes, of gums, and of resins are subjects which have attracted the attention of many investigators.

Pfeffer (16) in his "Physiology of Plants" states in general that mucilage may be formed by synthesis or by decomposition as when the cell wall becomes mucilaginous. He also accepts the doctrine that mucilage is often formed in the interior of the cell. Karsten (7) claims that the formation of cork, gum, slime, etc., s due to processes of intussusception going on in the protoplasm. Tschirch (21) has emphasized the conclusion that in the cell wall there is a specialized layer next the cuticle which he calls the resinogenous layer and in which so-called secretions are formed.

Of the earlier investigators, Cramer (2), Von Mohl (22), Nägeli (15), Hofmeister (6), Wigand (24), Schlacht (17), Frank (4), and De Bary (3), were of the opinion that mucilage building is a disorganization process occurring in the cell wall. The transformation into mucilage they all agreed began in the outer part of the wall and worked toward the inside. Hofmeister (6) believed that the cell walls became thickened by the apposition of new layers, hence the striated appearance of the jelly. Frank (4) found that in the bulbs of orchids mucilage developed from the cell contents in a crystal-bearing cell about a bundle of crystals which finally disappear. In other plants he thought the gum was formed

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from the cell wall. He noted that at first these gum cells contained starch grains, many of which appeared corroded.

Prillieux (17), in the gummosis of fruit trees, claims that gum may appear in cells whose walls do not show a trace of disorganization. The starch grains simply disappear and small masses of gum take their place. Haberlandt (5), in his treatment of the anatomy of cells containing slime from a morphological viewpoint, considers the slime masses in Malvaceae, Marchantiaceae, Cactaceae, and Lauraceae to be a very strongly thickened and finely stratified cell membrane. According to Haberlandt (5), in such cases the primary cell wall, as a rule, does not degenerate.

In 1893 Walliczek (23), working under Tschirch, concluded that there were cell content slimes as well as membrane slimes, but that cell content slime had been proved only for *Orchis* and *Symphytum*. He found that the cell content slimes appeared as homogeneous masses, while the membrane slimes were stratified. The following year Schilling (19), working on the question of slime formation in water plants, decided that slime building went on at the expense of the cell wall and that at the end of the process only a very thin shell was left about the cell.

Butler (1), studying gummosis in fruit trees, accepts the view that the process of gum formation is a degeneration of the cell wall. The essential factors are relative rate of growth and water supply. Dissolution begins in the secondary lamella and almost coincidently in the primary membrane, and the cell contents are at no time actively concerned in gum formation.

We now turn to a consideration of the investigations that have been made relating to the formation of mucilage in the cacti. These plants have been rather exhaustively studied for many years but so far comparatively little cytological work has been done upon the group. In most of the forms mucilage is very abundant. The question as to the method of its formation was discussed first by Meyen (14) in 1837. He reported that he found mucilage in the intercellular spaces of the cacti and in some cases he found mucilage ducts in great numbers. He concluded that a direct transformation of cell contents into mucilage took place and showed a figure with cells filled with mucilage.

Two years later Schleiden (20) published the results of the

first attempted cytological study of the cacti. He noted that the contents of the parenchyma cells was primarily "starch or mucilage in globules." Both were almost always surrounded with chlorophyll. In almost all species which he studied he reported that he found two to six times enlarged cells distributed in the cortex and in the central parts of the stem, all of which were totally filled with a vegetable jelly with a characteristic type of organization. These mucilage-filled cells he said he could not find in *Rhipsalis rhombea*, but in their place he found large cells filled with starch.

Between this work of Schleiden (20) in 1837 and that of Lauterbach (8) in 1889, no very full study of the mucilage of the cacti is reported. Cramer (2) described the slime of the cacti arising as a thickened layer on the cell wall, thus proving, as he held, its close relationship with cellulose. He found these continuous thickening layers in especially large single cells. He believed that by rupture the wall layers became irregular and showed such a structure as Schleiden (20) described.

Schacht (18) studied old stems of *Opuntia Ficus-indica* and reported gum-like tragacanth contained in canals. He believed that this gum arose as the result of a disorganization of the cell wall. Wigand (24) observed that certain parenchyma cells in the cacti, which were of somewhat greater diameter than their neighbors, were filled with a homogeneous colorless slime. De Bary (3) noted that this mass of mucilage had the structure of a very thick, abundantly, and delicately stratified cell wall. He concluded that it was the cell wall thickened at the expense of the internal cavity of the cell.

From his investigations Lauterbach (8) was led to believe that there are two methods by which the mucilage is formed, one holding true for *Opuntia*, and the other for the remainder of the cactus groups. In the *Opuntia* the mucilage arises in a cell containing a small crystal of some oxalate. This crystal, as he thought, seemed to stimulate the growth of the cell. Later the nucleus and crystal might appear suspended on strands of cytoplasm in the midst of the cell and mucilage would then begin to appear in the periphery of the protoplasm.

In the other cacti he held that the mucilage also arose in the

periphery of the protoplast in the plasma membrane, but that no crystal was present. The cytoplasm is pressed toward the center of the cell as the mucilage increases until it remains as a mere remnant in the interior. By the use of a strong sugar solution he was able to make the mucilage surrounded by its delicate plasma envelope pull away from the wall. He observed striations in the mucilage, but made no attempt to account for their origin.

Walliczek (23) claims that the mucilage of the cacti arises as a secondary thickening of the primary cell wall. He also states that it does not give a cellulose reaction in the moment of its formation nor later. He suggests that the stratification in most cases is dependent upon a different water content in the layers. This stratification, he says, shows best when the material is preserved in alcohol and water added later.

Longo (11, 12) holds that the peculiar structure of the mucilage which Walliczek describes is due to the action of the alcohol which, he believes, withdraws water from the mucilage. He used fresh material as well as alcoholic preparations and found that the mucilage was not the result of a transformation of the cellulose membrane, but came from the protoplasm, showing the characteristics of mucilage as soon as it appeared. He does not agree with Lauterbach (8) that the mucilage is produced in droplets in the parietal protoplasm. He finds it appearing between this and the thin cell, wall of cellulose, which never undergoes any modification.

As to whether the mucilage arises from the wall or from the protoplasm, the opinions seem to be about equally divided, but Walliczek, Lauterbach, and Longo all agree that it is accumulated between the plasma membrane and the cell wall. In this connection I might say that in the present paper I have figured a case in which the wall between a mucilage cell and the neighboring cell shows the middle lamella with the wall of equal thickness on each side of the lamella, which is good evidence that the wall is not affected by the formation of the mucilage.

For the most part I have studied *Rhipsalis rhombea* (from the New York Botanical Garden), the species in which Schleiden (20) said he could not find any cells filled with mucilage. Owing to the incompleteness of his record it is impossible to determine whether

or not his *Rhipsalis rhombea* was identical with the species which I used. My plants are all from greenhouse sources and were probably introduced from Europe. Besides *Rhipsalis rhombea*, I have used *Rhipsalis pachyptera* and *Rhipsalis Houlletiana*, brought from France, likewise *Opuntia inermis* and *Pereskia Pereskia*.

In the leaves of the flower buds of *Opuntia* and of *Rhipsalis*, the mucilage cells are often so large and so numerous that in cross section these leaves seem to be almost filled with mucilage. With the Flemming triple stain the mucilage is colored blue, but is not so deep a blue as the starch grains. The mucilage is never, with the method I have used, of the same color as the wall surrounding it.

In the flower buds of *Rhipsalis* the large mucilage cells are abundant, not only in the floral leaves but also in the ovary wall, in some cases almost every cell being filled with mucilage. The mucilage cells are more numerous in the periphery than toward the center. Sections were made also of very young *Rhipsalis* stems. In these meristematic tissues there are numerous mucilage cells which are two or three times as large as the neighboring cells. The adjacent cells (FIG. 1) are typical vegetative cells containing a large central vacuole surrounded by a thin layer of cytoplasm adhering to the cell wall. In it are suspended the nucleus and a few starch grains.

On the other hand, in the large cell (FIG. 2), before any mucilage appears, the cytoplasm is much more dense. While it is spongy and vacuolated, there is no large central vacuole, neither is there any starch as a rule. The cells at this stage contradict entirely the possibility suggested by Lloyd (**9**) that their large size is due to imbibition of water by the mucilage which they contain. In the species studied by me, the cells destined to form mucilage reach a diameter two or three times that of adjoining cells before the mucilage begins to form in them. In FIG. 3 the protoplast is surrounded by a layer of mucilage, but its diameter inside the mucilage layer is approximately the same as that of the protoplast in Fig. 2.

The growth in these cells at this stage is true growth and not at all a mere matter of increased water content of a central vacuole.

As noted, their cytoplasm is especially dense and their nuclei and nucleoles proportionately large and very highly stainable, as shown in FIGS. 2 and 3. Their growth is plainly a matter of the accumulation of largely increased amounts of protoplasm preparatory to their secretory activity in the production of mucilage. While there is plenty of evidence for believing that the cells increase in size during the period of mucilage production and possibly after they are completely filled, their increase in size before there is any evidence of the presence of mucilage in them is equally clear. A glance at FIG. 2 will show the number of cells which adjoined this large cell and will give some idea of how these hypertrophied cells, which are to form mucilage, compare in size with their neighbors. FIG. 1 shows one of the ordinary cells adjoining a mucilage cell.

The mucilage or slime appears first as a very thin homogeneous film lying between the cell wall and the cytoplasm (FIG. 3). It stains but slightly and nowhere shows any conspicuous colloidal organization. In some of the older cells this layer persists about the periphery, while the remainder of the mucilage looks somewhat fibrillar and is also vacuolated (FIG. 5); in other cells the strands and vacuoles extend almost to the cell wall (FIG. 4).

As the amount of mucilage increases the cytoplasm is apparently crowded in toward the center of the cell, the nucleus and nucleole become smaller (FIG. 4), and while this is taking place both cytoplasm and nuclear-plasm become denser and lose their characteristically differentiated structure. Finally the nuclear membrane disappears and also the nucleole as such and the nuclear-plasm becomes merely a denser mass within the compressed and granular cytoplasm (FIG. 5). In the end nothing remains of the protoplasmic contents of the cell but an irregular highly stainable mass in about the middle of the cell. Sometimes this mass appears in section as a rather straight line, sometimes it has in section the shape of the letter Y. Many cells are also found which show no remnant whatever of the cytoplasm.

In the cells which are completely filled or nearly so, without exception the mucilage has the organization of a spongy substance full of vacuoles. Between and through these vacuoles there extend films, strands, or even threads, which radiate outward from

the cytoplasm in a rather characteristic fashion (FIG. 4). In some cells the mass of mucilage is rather homogeneous throughout, in many others it is reticulated and zoned (FIG. 7), so as to have led some investigators to believe that it is the much thickened and stratified cell wall.

While the cytoplasm with its included starch disappears entirely the cell wall nowhere shows a breaking down or disorganization. At the end of the process it is just as thick as at the beginning. In favorable cases the middle lamella is discernible and in such preparations the secondary wall is seen everywhere intact and is just as thick and no thicker on the side of the lamella next the mucilage cell than on the opposite side (FIG. 6). This would seem to show that the wall does not become disorganized or changed in any way as the formation of mucilage proceeds. The evidence all seems to point in one direction, namely, that mucilage in the cacti is formed not at the expense of the cell wall, but at the expense of the cytoplasm and nucleus. Neighboring cells, as well as the mucilage cell, perhaps, contribute of their content. They at any rate become flattened and contain very little cytoplasm (FIG. 5).

Haberlandt (5) has pointed out that in many cases slime containers may serve as water reservoirs and that it is not necessary to regard such slimy cell content as a useless excretion. He notes that the early differentiation of the slime cells in the vicinity of the growing point appears to point to their having a mechanical function in the growth process, and suggests that we have to do here with "Schwellapparaten."

This observation is perhaps borne out by experiments by MacDougal and others at the Tucson laboratory. It will be recalled that in his work on colloid hydratation and growth in the cacti, Long (10) reported that, in general, growth and swelling paralleled each other rather closely. Later MacDougal (13) found that agar, composed of pentoses presumably having some qualities identical with those of the plant mucilages, and both young and old disks of *Opuntia* will swell more when placed in distilled water or an alkaline solution than when placed in an acid solution. He found also that the apical parts of joints showed greater capacity for absorption than the basal portions. In a series of similar imbi-

bition experiments with joints of *Rhipsalis*, I have found that the greatest swelling in a majority of cases takes place in the apical region, the region of growth and of abundant mucilage cells.

We have then in the cacti a transformation of the content of many cells in the growing regions into a mucilage which, by absorbing water, may simulate true growth and may be of importance in conserving and regulating the supply of water for the growing cells themselves. As to the method of formation of the mucilage, as I have noted it in the cacti and more particularly in *Opuntia* and in *Rhipsalis*, it is the nucleus and cytoplasm that are the active agents. Apparently the cell wall is at no time involved in the process. The mucilage comes from the cytoplasm and the formation begins between the cell wall and the protoplasm, as Longo (**11**, **12**) points out. As the mucilage increases the nucleus and cytoplasm decrease in size and may entirely disappear, leaving the enlarged cell completely filled with mucilage.

That all resins, gums, and mucilages are similarly formed is in no sense suggested, but it is of interest that we have in these mucilage cells of the cacti a method of secretion much more like that of the gland cells of animals than the more familiar method by a resinogenous layer of the cell wall as found in many trichomes.

In concluding, I wish to express my gratitude to Dr. R. A. Harper of Columbia University, under whose direction this work was carried out, for his helpful criticisms and suggestions.

DEPARTMENT OF BOTANY,
COLUMBIA UNIVERSITY

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Explanation of plate 8

FIG. 1. Cell from a section of a very young stem of *Rhipsalis rhombea* showing cytoplasm about the periphery containing starch grains and nucleus. Magnification about 1,900 diameters.

FIG. 2. Cell adjoining that shown in FIG. 1, showing the first stage in the formation of a mucilage cell. Nucleus and nucleole are much enlarged, cell is filled with cytoplasm, no starch is present. Magnification about 1,900 diameters.

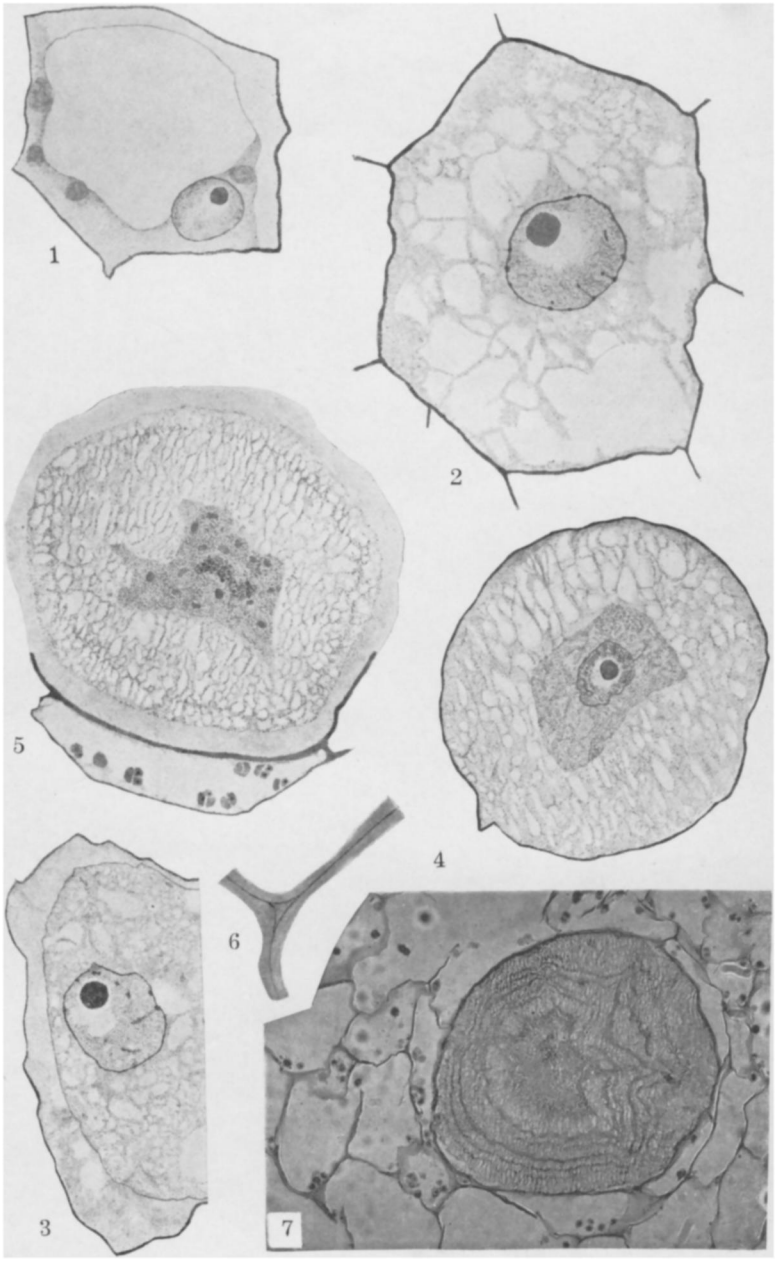
FIG. 3. Cell from a section of a young stem of *Rhipsalis rhombea*. A large nucleus and nucleole are present and the cytoplasm is spongy, as in FIG. 2. A narrow border of mucilage like a thin film lies between the cell wall and the cytoplasm. Magnification 1,300 diameters.

FIG. 4. Mucilage cell from the ovary wall of a bud of *Rhipsalis Houlletiana*. The cytoplasm is compressed to a small mass in the center of the cell, its organization lost, but the nucleus still persisting. Alveolar mucilage fills the space between the cell wall and the cytoplasm. Magnification 600 diameters.

FIG. 5. Mucilage cell from a flower bud of *Rhipsalis pachyptera*. The cytoplasm lies in the central part of the cell and is very much compressed. A few starch grains still persist, but nucleus and nucleole are disintegrated. Magnification 600 diameters.

FIG. 6. Section of a wall between a mucilage cell and two adjoining cells in a flower bud of *Rhipsalis pachyptera*, showing the middle lamella. Magnification 1,100 diameters.

FIG. 7. Photograph of a section from a flower bud of *Rhipsalis pachyptera* showing the zonation in a mucilage cell. The darker central portion is cytoplasm, the striations in the mucilage being nearly parallel to it.



STEWART: MUCILAGE OR SLIME FORMATION IN THE CACTI